

Fischerpietteus, a New Genus of Streptaxid Land Snails from Northern Madagascar

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Abstract. *Fischerpietteus*, gen. nov. is anatomically streptaxid and is diagnosed by its circular and unreflected peristome, regular coiling, deep sutures, broad umbilicus, small size (shell diameter 2.1–4.6 mm), and relatively faint sculpture. The genus contains six species, all newly discovered. Intraspecific shell variation is remarkable and is associated with altitude. *Fischerpietteus*, gen. nov. is the third streptaxid genus/subgenus believed to be endemic to Madagascar, and is the only one of Madagascar's seven native streptaxid genera (comprising 206 known native species) that is low-spired.

INTRODUCTION

This paper is one in a series reporting taxonomic results from the author's 1992–1996 survey and inventory of Madagascar's land mollusks.

Madagascar's streptaxid fauna is especially rich. Eighty species and eight subspecies of *Gulella* Pfeiffer, 1856 (*sensu* Fischer-Piette et al., 1994), are now known (Emberton, 2001a, 2002). *Parvedentulina* Emberton & Pearce, 2000, now comprises 94 species (Emberton, 2002). Other genera (and subgenera) represented are *Edentulina* Pfeiffer, 1856 (12 species, including one introduced; Emberton, 1999), *Streptostele* (*Makrokonche*) Emberton 1994 (seven species, including *S. (M.) latembryohelix* Emberton & Pearce, 2000, transferred from *Parvedentulina* by Emberton, 2001b; Emberton, 1994; Emberton & Pearce, 2000), *Fischerpietteus*, gen. nov. (six species herein described), *Gonospira* Swainson, 1840 (five species described to date; Fischer-Piette et al., 1994), *Streptostele* (*Raffraya*) Bourguignat, 1883 (two species; Fischer-Piette et al., 1994), and *Pseudelma* Kobelt, 1904 (one species; Fischer-Piette et al., 1994), as well as the two introduced genera *Indoennea* Kobelt, 1904 (one species, *I. bicolor* [Hutton, 1834] = "*Gulella bicolor*" of Fischer-Piette et al., 1994, and Emberton, 2001), and *Gonaxis* Taylor, 1877 (one species, *G. kibweziensis* [Smith, 1894]).

In sum, Madagascar's streptaxid fauna as currently known comprises seven native genera, 206 native species, eight native subspecies, two introduced genera, and three introduced species. Three of its streptaxid genera and subgenera seem to be endemic to Madagascar: *Fischerpietteus*, gen. nov., *Parvedentulina*, and *Streptostele* (*Makrokonche*). *Fischerpietteus*, gen. nov. is Madagascar's only known native streptaxid genus that is low-spired.

LOCALITIES

Of the 1126 stations collected throughout Madagascar in 1992–1996, only 63 stations in 11 transects, all northern, yielded *Fischerpietteus*, gen. nov. Station numbers are in the author's "MBI" series.

169–194. Mt. d'Ambre (5 stations, 1200–1400 m). 169, 172. montane hardwood rainforest, 8 July 1995. 169. 12°32'E, 49°10'S, 1200 m. 172. 12°35'E, 49°09'S, 1325 m. 188–194. rainforest. 188. 12°35'E, 49°09'S, 1400 m, 11 July 1995. 193, 194. rainforest, 12 July 1995, 12°34'E, 49°09'S. 193. 1305 m. 194. 1280 m.

256, 257. S of Vohimar (2 stations, 70–90 m), 13°35'E, 49°59'S, viny rainforest, 2 September 1995. 256. 90 m. 257. 70 m.

260–262. Mt. Ambalanirana (3 stations, 400–561 m), N of Sambava, 13°50'E, 49°59'S. 260, 261. rainforest. 260. 561 m, 3 September 1995. 261, 262. 4 September 1995. 261. 500 m. 262. viny rainforest, 400 m.

418. Andavakoera massif (1 station, 115 m), N of Bet-siaka, 13°06'E, 49°13'S, dry deciduous forest, 115 m, 31 August 1995.

513–527. W Tsaratanana Reserve (5 stations, 1395–1905 m). 513. 13°59'E, 48°47'S, rainforest, 1525 m, 14 June 1995. 519, 524. 13°59'E, 48°48'S, 16 June 1995. 519. cloudforest, 1905 m. 524. bamboo forest, 1715 m. 526, 527. 13°59'E, 48°47'S, rainforest, 17 June 1995. 526. 1500 m. 527. 1395 m.

565. Ankarana Reserve (1 station, 40 m), 12°55'E, 49°05'S, dry deciduous forest, 40 m, 22 August 1995.

587–610. Mt. Marojejy (10 stations, 720–1405 m). 587–593. rainforest. 587. 14°25'E, 49°45'S, 720 m, 13 September 1995. 593–601. 14°26'E, 49°44'S. 593–597. 14 September 1995. 593. 1300 m. 597, 601. cloudforest. 597. 1405 m. 601. 1800 m, 15 September 1995. 605–636. rainforest. 605–609. 14°26'E, 49°45'S. 605–607. 16 September 1995. 605. 1200 m. 606. 1100 m. 607. 1150

m. 608–610. 17 September 1995. 608. 1000 m. 609. 900 m. 610. 14°25'E, 49°45'S, 800 m.

620–649. Mt. Marojejy-Kely (14 stations, 655–1384 m). 620. 14°30'E, 49°34'S, 655 m, 23 September 1995. 625. 14°29'E, 49°35'S, 850 m, 24 September 1995. 627–638. 14°28'E, 49°35'S. 627–634. 25 September 1995. 627. 900 m. 629. 1000 m. 631. 1125 m. 633. 1200 m. 634. 1170 m. 636–639. 26 September 1995. 636. 1260 m. 638. cloudforest, 1280 m. 639. 14°27'E, 49°35'S, scrub, 1384 m. 643–649. rainforest. 643–645. 14°28'E, 49°33'S, 27 September 1995. 643. 1085 m. 645. 960 m. 648, 649. 28 September 1995. 648. 14°29'E, 49°33'S, 805 m. 649. 14°29'E, 49°34'S, rainforest, 700 m.

659–674. Mt. Ambatosoratra (9 stations, 880–1500 m), 14°32'E, 49°42'S. 659–664. rainforest. 659–662. 4 October 1995. 659. 1000 m. 661. 1100 m. 662. 940 m. 664–671. 5 October 1995. 664. 1050 m. 666, 668. cloudforest with bamboo. 666. 1400 m. 668. 1500 m. 671–674. rainforest. 671. 1300 m. 673, 674. 6 October 1995. 673. 1200 m. 674. 880 m.

688–709. Mt. Anjanaharibe-Anivo (11 stations, 910–1980 m). 688–694. 14°44'E, 49°26'S. 688. cloudforest, 1400 m, 19 October 1995. 689–696. 20 October 1995. 689. rainforest, 1300 m. 692. cloudforest, 1600 m. 694. bamboo cloudforest, 1800 m, 20 October 1995. 695. 14°43'E, 49°25'S, cloudforest, 1980 m. 696–699. bamboo cloudforest. 696. 14°44'E, 49°25'S, 1900 m. 699, 700. 14°44'E, 49°26'S, 21 October 1995. 699. 1520 m. 701, 701. cloudforest. 700. 1700 m. 701, 702. 14°44'E, 49°27'S, 22 October 1995. 701. 1505 m. 702, 709. rainforest. 702. 1400 m. 709. 14°46'E, 49°28'S, 910 m, 24 October 1995.

756, 758. Ambatovaky Reserve (2 stations, 605–675 m). 756. 16°44'E, 49°10'S, rainforest with pandanus, 675 m, 22 November 1995. 758. 16°42'E, 49°10'S, rainforest, 605 m, 23 November 1995.

MATERIALS AND METHODS

Materials were collected in 1995 using methods recommended for Madagascan rainforests by Emberton et al. (1996). Generic identification and comparisons were made using Zilch (1959–1960), Bruggen (1967, 1989), Tillier (1989), Verdcourt (1990), Emberton (1994), Gerlach (1995), and Gerlach & Bruggen (1999). Measurements were made following methods of Emberton & Pearce (2000), using an ocular micrometer on a Wild M3C dissecting microscope.

Dissections were on black wax under 70% ethanol. The type species of the genus was dissected for the purpose of describing the genus anatomically. Other species were investigated only conchologically, in order to speed publication of this report because of Madagascar's environmental crisis.

An initially baffling degree of shell variation was assessed as follows. For each altitudinal transect from

which sufficient measurable samples were available, high- and low-altitude shells were compared for: coiling tightness (whorl count divided by natural logarithm [\ln] of shell diameter); height/diameter; embryonic coiling tightness (diameter of first 1.5 whorls); aperture relative size (apertural inside diameter divided by whorl count); embryonic whorl count; number of whorls of smooth embryonic sculpture before first appearance of sutural notches; umbilicus diameter/shell diameter; relative strengths of axial ribs on body-whorl sutural, peripheral, and umbilical regions; relative strengths of embryonic axial grooves and spiral lines; and relative depth of sutural groove on body whorl. Means and standard deviations of those shell variables were tabulated and visually compared to determine altitudinal and geographic trends within and among species. Every attempt was made to apply Templeton's (1989) cohesion concept in diagnosing species.

SYSTEMATICS

Higher classification follows Ponder & Lindberg (1997; suborder and above), Nordsieck (1986; infraorder), and Vaught (1989; superfamily and family).

Class GASTROPODA

Clade HETEROBRANCHIA

Subclass PULMONATA

Order STYLOMMATOPHORA

Suborder SIGMURETHRA

Infraorder ACHATINIDA

Superfamily STREPTAXOIDEA

Family STREPTAXIDAE

Fischerpietteus Emberton, gen. nov.

Type species: *Fischerpietteus edouardi*, sp. nov.

Other species: *F. ambrensis*, sp. nov., *F. ambatovakiae*, sp. nov., *F. ankaranae*, sp. nov., *F. minutus*, sp. nov., *F. vohimarae*, sp. nov.

Diagnosis: Among streptaxids, unique in its combination of circular, unreflected peristome; deep suture; and broad umbilicus. Also diagnostic are its very small size (shell diameter 2.1–4.6 mm), regular coiling, and relatively faint sculpture.

Comparisons: The unreflected peristome, regular coiling, very small size, and open umbilicus are shared by the streptaxid genera *Augustula* Thiele, 1931; *Imperturbatia* Martens in Martens & Wiegman, 1898; *Martinella* Jousseaume, 1887; et al., but those have distinctly angular or otherwise non-rounded peristomes, shallow sutures, and

much narrower umbilici, and genera from the Seychelles in addition have strong sculptures.

Other land-snail families such as zonitids, rhytidids, and charopids can have similar shells, but *Fischerpietteus*, gen. nov. differs from them anatomically, so far as is known. Taken together, absence of jaw, elongate buccal mass, daggerlike radular teeth, penial sheath incorporating convoluted portion of vas deferens, penis armed with dark chitinous spines, and distinctive configuration of central nervous system, seem to place *Fischerpietteus*, gen. nov. firmly within streptaxids.

Shell description, based on 57 shells from 31 stations in 11 transects (Table 1): Diameter 2.1–4.6 mm; height/diameter 0.5–0.8; whorls 4.6–5.8, regularly increasing, whorls/*ln* diameter 3.35–6.34; umbilicus/diameter 0.23–0.37. Spire low-conic to domed-conic. Body-whorl periphery rounded, rarely with trace of angulation. Suture deeply impressed, simple or within a spiral groove; whorl shoulders rounded. Apertural lip unreflected. Aperture circular, without downward deflection; apertural inside width/whorl count 0.15–0.33. Embryonic whorls 1.8–2.1; first 1.5 whorls 0.63–0.83 mm in diameter. Embryonic sculpture with—rarely without—sutural notches (short, narrow grooves extending downward from and perpendicular to the suture) that begin after 0.7 to 1.7 smooth whorls, but, rarely, can start immediately at 0.0 whorl; embryonic sculpture also may include relatively faint axial grooves and/or spiral lines. Body-whorl sculpture consisting of fairly regular axial riblets, never very strong, rarely very faint to trace. Color uniform whitish or light yellow to yellow-green, translucent in fresh shells.

Anatomy, based on four paratypes of type species, from two localities (Figures 5–13): Foot long and narrow, sole smooth and undivided. Single, indistinct parapodial groove visible. Kidney sigmurethrous. Interior mantle collar edged with glandular tissue, extremely variable in size and mass.

Agathous. Buccal mass approximately twice as long as wide. Radular teeth (viewed at 80×) daggerlike. Single, large salivary gland.

Nerve ring fairly symmetrical. Cerebral commissure very short. Cerebropedal connectives long. Pedal ganglia relatively small but with large, conspicuous statocysts. Pleural ganglia close to pedals, obscure. Pleuroparietal connectives extremely long. Right and left parietal ganglia and visceral ganglion tightly bound together and possibly fused.

Genital pore (G) far posterior, under mantle collar. Penial retractor muscle (R) paralleling body retractor muscle (BR) and inserting adjacent it. Right tentacular retractor passing around, not between, male and female genital tracts. Lower reproductive system without dart sac or any other appendage. Atrium (A) small, sometimes indistinct.

Penis (P) about 2.4 mm in length, about 0.12–0.16 as wide as long, tapering at tip. Base of penis (P) surrounded

by muscular sheath (PS) into which portion of vas deferens (VD) incorporated as convoluted loop (Figure 12). Vas deferens (VD) otherwise fairly straight and unconvoluted, entering at penial (P) apex, where penial retractor muscle (R) also originates. Functional surface of penis (Figures 7, 13) sculpted with two parallel, adjacent, fleshy pilasters (PL1 and PL2), and with diamond-shaped pustules (PP), each bearing single, central, chitinous, dark brown spinule.

Vagina (V) fairly short and broad. Spermathecal duct (SD) very long and slender; spermatheca (S; = bursa copulatrix, gametolytic gland) ovoid, thin-walled, transparent, adjacent to proximal albumen gland (AG; Figure 10). Ovotestis (OT; Figure 11) consisting of clusters of acini nesting within apical digestive gland (D) and distributed regularly along, and ducting into, hermaphroditic duct (H). Hermaphroditic duct (H) very thin and unconvoluted. Fertilization pouch (F) a very long, single, tightly convoluted sac. Seminal receptacle (SR) partially embedded within albumen gland (AG), variable in size, visible when full as two clusters of saccules (Figure 10). Prostate-uterus (PU) and free oviduct (o) approximately equal in length. Oviparous; unlaidd eggs (E) in uterus spherical, approximately 0.9 mm in diameter.

Etymology: For the late Edouard Fischer-Piette, in grateful recognition of his 30 years of work on, and monographing of, the Madagascan land-snail fauna.

Gender: Masculine.

Shell variation and species designations: Measurable high- and low-elevation shells were available from seven transects: Ambalanirana, Marojejy, Marojejy-Kely, Ambatosoratra, Anjanaharibe, Tsaratanana, and Mt. d'Ambre (Table 1). Ambalanirana differed from the other six of these transects in being coastal, in having low overall altitude, and in its high-altitude sample being from the summit.

Despite remarkable shell variation, six of the transects (all but Mt. d'Ambre) showed enough overlap in all 13 measured characters that only a single species (*Fischerpietteus edouardi*, sp. nov., Figures 1–4) could be postulated for them (Table 1). The Mt. d'Ambre shells, however, showed sufficient disjunction from *F. edouardi*, sp. nov. in five characters (coiling tightness relative to spire height, aperture/whorls, umbilicus/diameter, peripheral axial rib strength, and sutural groove) to be designated a distinct species (*F. ambrensis*, sp. nov., Table 1).

Both *F. edouardi*, sp. nov. and *F. ambrensis*, sp. nov. showed major altitudinal differences in shell morphology (Table 2). On Mounts Marojejy, Marojejy-Kely, Anjanaharibe, and d'Ambre, shell coiling was substantially looser at higher altitude. This looser coiling was associated with a distinctly flatter spire (decreased height/diameter) at higher altitudes on three of the mountains. However, on Mount Ambalanirana—and to a lesser extent along the

Table 1

Shell-measurement means (and standard deviations) for different species, transects, and altitudes. Altitudes in meters. Abbreviations: (s) summit, #St Number of stations, m-s moderate to strong, n Number of shells, vWk very weak, w-m weak to moderate, wk-m weak to moderate. See text for explanations of variables.

Species	Transect	Altitude	#St	n	Coiling tightness	Height/Diameter	Diam. 1st 1.5 whorls	Aperture/ No. whorls	Embryonic No. whorls	1st Embryonic SutNotches
edouardi	Ambalanirana	400–500	1	2	3.98 (.02)	0.65 (.00)	0.72 (.02)	0.26 (.01)	1.95 (.07)	1.55 (.21)
edouardi	Ambalanirana	561 (s)	2	2	4.24 (.01)	0.72 (.06)	0.68 (.00)	0.25 (.01)	1.90 (.00)	1.30
edouardi	Marojejy	900	1	3	3.87 (.05)	0.63 (.02)	0.75 (.05)	0.26 (.01)	1.83 (.03)	1.30 (.20)
edouardi	Marojejy	1100	1	3	3.45 (.10)	0.59 (.03)	0.80 (.01)	0.31 (.01)	1.93 (.06)	1.03 (.06)
edouardi	Marojejy-Kely	900–1085	3	3	4.17 (.12)	0.74 (.04)	0.73 (.04)	0.25 (.01)	1.87 (.06)	1.37 (.06)
edouardi	Marojejy-Kely	1280	1	3	3.66 (.12)	0.67 (.01)	0.80 (.03)	0.30 (.02)	1.85 (.07)	1.05 (.07)
edouardi	Ambatosoratra	880	1	2	3.95 (.17)	0.65 (.04)	0.76 (.04)	0.26 (.01)	1.83 (.04)	1.20 (.14)
edouardi	Ambatosoratra	1300–1500	2	4	3.85 (.10)	0.64 (.04)	0.74 (.01)	0.28 (.02)	1.91 (.06)	1.50 (.00)
edouardi	Anjanaharibe	910–1300	2	5	3.58 (.09)	0.60 (.04)	0.79 (.04)	0.28 (.01)	2.01 (.06)	1.03 (.05)
edouardi	Anjanaharibe	1980	1	2	3.42 (.09)	0.61 (.02)	0.79 (.06)	0.33 (.01)	2.10	1.15
edouardi	Tsaratanana	1395	1	2	3.73 (.08)	0.58 (.03)	0.78 (.03)	0.29 (.02)	1.95 (.07)	1.50 (.00)
edouardi	Tsaratanana	1715–1905	2	4	3.90 (.10)	0.61 (.07)	0.79 (.03)	0.29 (.01)	1.93 (.11)	1.43 (.05)
vohimarae	S of Vohimar	70–90	2	2	3.77 (.18)	0.56 (.04)	0.75 (.01)	0.25 (.00)	1.90 (.00)	none (.00)
ankaranae	Ankarana	40	1	1	4.50	0.70	0.76	0.23	1.80	—
ambrensis	Mt. d’Ambre	1200–1280	2	2	4.28 (.08)	0.61 (.03)	0.71 (.04)	0.22 (.00)	1.93 (.04)	1.30
ambrensis	Mt. d’Ambre	1305–1325	2	4	4.11 (.08)	0.56 (.01)	0.74 (.03)	0.22 (.01)	1.89 (.03)	1.43 (.12)
ambrensis	Andavakoera	115	1	3	4.23 (.23)	0.56 (.02)	0.68 (.02)	0.21 (.02)	1.87 (.03)	1.30 (.28)
ambatovakiae	Ambatovaky	605–675	2	2	5.28 (.09)	0.67 (.08)	0.69 (.01)	0.19 (.02)	1.90 (.07)	0.00
minutus	Marojejy	900	1	4	6.15 (.16)	0.71 (.03)	0.66 (.02)	0.15 (.01)	1.94 (.05)	0.78 (.05)
minutus	Marojejy-Kely	700	1	2	6.23 (.16)	0.74 (.01)	0.64 (.01)	0.15 (.00)	1.90 (.00)	0.78 (.04)
minutus	Tsaratanana	1500	1	2	5.50 (.06)	0.62 (.03)	0.67 (.02)	0.17 (.00)	1.95 (.00)	0.75 (.00)

Tsaratanana transect—this trend was reversed (tighter coiling and higher spire at the summit; Table 2).

Not only coiling tightness and spire height, but all other measured shell variables showed distinct altitudinal trends (Table 2). Embryonic coiling (= diameter of first 1.5 whorls) tended to be tighter, and aperture size tended to be greater at higher altitudes (two transects and four transects, respectively; both trends reversed on Ambalanirana). On three transects each, higher altitudes were associated with smaller umbilici and increased embryonic whorls (the latter trend reversed on Mt. d’Ambre). First appearances of embryonic sutural notches differed with altitude on all seven transects, increasing on three and decreasing on four (Table 2).

Thus much of the enormous shell variation in *Fischerpietteus*, gen. nov. was associated with altitude. It is beyond the scope of this paper to propose and test hypotheses on the causes of these trends. The present purpose of Tables 1 and 2 is only to provide guidelines for detecting, diagnosing, and describing species.

Key to Species of *Fischerpietteus*

- 1a. Shell minute and very tightly coiled: adult diameter 2.1–2.7 mm, whorls/*ln* diameter 5.2–6.3 2
- 1b. Shell larger and more loosely coiled: adult di-

- ameter 2.9–4.6 mm, whorls/*ln* diameter 3.3–4.5 3
- 2a. Coiling looser: whorls/*ln* diameter 5.2–5.3 at 605–675 m altitude; embryonic sutural notches appear immediately, at 0.0 whorls; shell periphery rounded ***F. ambatovakiae***
- 2b. Coiling tighter: whorls/*ln* diameter 5.9–6.3 at 700–900 m altitude, 5.4–5.5 at 1500 m; embryonic sutural notches first appear at 0.7–0.8 whorls; shell periphery slightly angulate ***F. minutus***
- 3a. No embryonic sutural notches; body-whorl axial ribs very weak to absent at suture; umbilicus broad, 0.36–0.37 shell diameter, and body-whorl suture at most slightly recessed within a spiral groove ***F. vohimarae***
- 3b. Embryonic sutural notches present; body-whorl axial ribs weak to moderate, clearly present, at suture; umbilicus narrower, 0.23–0.32 shell diameter, or, if broad, body-whorl suture moderately to pronouncedly recessed within a spiral groove 4
- 4a. Tight coiling, high spire, small umbilicus, and body-whorl axial ribs weak at periphery and umbilicus (whorls/*ln* diameter 4.50, height/diameter 0.70, umbilicus/diameter 0.26) ***F. ankaranae***

Table 1
Extended.

Species	Transect	Elevation	#St	n	Umbilicus /Diameter	AxialRibStrng			EmbryonPeriphSculpt		
						Sutr	Prph	Umbl	AxGroovs	SpirLines	SutGroove
edouardi	Ambalanirana	400–500	1	2	0.30 (.03)	mod	mod	mod	none-mod	none	slight
edouardi	Ambalanirana	561 (s)	2	2	0.29 (.02)	mod	mod	mod	none	none	slight
edouardi	Marojejy	900	1	3	0.28 (.02)	mod	mod	mod	slgt-mod	slight	slight
edouardi	Marojejy	1100	1	3	0.28 (.02)	mod	mod	mod	moderate	none	slight
edouardi	Marojejy-Kely	900–1085	3	3	0.28 (.04)	mod	mod	mod	none-slgt	slight	slight
edouardi	Marojejy-Kely	1280	1	3	0.25 (.02)	mod	mod	mod	none-slgt	none-slgt	slight
edouardi	Ambatosoratra	880	1	2	0.29 (.00)	mod	mod	mod	slgt-mod	none	slight
edouardi	Ambatosoratra	1300–1500	2	4	0.26 (.02)	mod	mod	mod	slgt-mod	none-slgt	slight
edouardi	Anjanaharibe	910–1300	2	5	0.29 (.02)	mod	m-s	mod	none-slgt	slgt-mod	slight
edouardi	Anjanaharibe	1980	1	2	0.27 (.01)	mod	m-s	mod	slight	slight	slight
edouardi	Tsaratana	1395	1	2	0.31 (.01)	mod	mod	wk-m	slight	none	slight
edouardi	Tsaratana	1715–1905	2	4	0.26 (.02)	mod	mod	wk-m	slight	none	slight
vohimarae	S of Vohimar	70–90	2	2	0.37 (.01)	vWk	weak	vWk	slgt-mod	none	slight
ankaranae	Ankarana	40	1	1	0.26	mod	weak	weak	—	—	moderate
ambrensis	Mt. d’Ambre	1200–1280	2	2	0.34 (.01)	w-m	weak	weak	none	verySlgt	pronounced
ambrensis	Mt. d’Ambre	1305–1325	2	4	0.34 (.01)	mod	weak	weak	none-slgt	none	pronounced
ambrensis	Andavakoera	115	1	3	0.36 (.02)	w-m	weak	vWk	none	none	moderate
ambatovakiae	Ambatovaky	605–675	2	2	0.25 (.03)	mod	mod	weak	slight	none	slight
minutus	Marojejy	900	1	4	0.28 (.01)	mod	mod	w-m	slight	none-slgt	moderate
minutus	Marojejy-Kely	700	1	2	0.30 (.02)	mod	mod	weak	slight	none	moderate
minutus	Tsaratana	1500	1	2	0.30 (.04)	mod	mod	mod	slgt-mod	none-slgt	slight

- 4b. Looser coiling or, if tight, spire low (h/d 0.58) and umbilicus large (u/d 0.38), or spire higher (h/d 0.79) and body-whorl axial ribs moderately strong at periphery and umbilicus 5
- 5a. Coiling tighter and spire low (whorls/*ln* diameter 4.01–4.48, height/diameter 0.54–0.63); aperture smaller (aperture/whorl count 0.19–0.23); umbilicus broader (umbilicus/diameter 0.32–0.38); peripheral axial ribs weak; body-whorl suture lying within a moderate to pronounced spiral groove *F. ambrensis*

- 5b. Coiling generally looser (whorls/*ln* diameter 3.34–3.99), but when tight (whorls/*ln* diameter 4.00–4.31), spire higher (height/diameter 0.68–0.75); aperture larger (aperture/#whorls 0.24–0.32); umbilicus narrower (umbilicus/diameter 0.23–0.32); peripheral axial ribs moderate to strong; body-whorl sutural groove slight at most *F. edouardi*
- Species descriptions:* Types are in the Florida Museum

Table 2

Changes in mean values of shell variables with increasing altitude along seven transects (calculated from Table 1). Differences shown are equal to at least one (of the larger) standard deviation; * at least two standard deviations; ** at least three standard deviations.

Species	Transect	Coiling tightness	Height/Diameter	Diam. 1st 1.5 whorls	Aperture/No. whorls	Embryonic No. whorls	1st Embryo SutNotch	Umbilicus /diameter
edouardi	Ambalanirana	+0.26**	+0.07	-0.04*	-0.01	—	-0.25	—
edouardi	Marojejy	-0.42**	-0.04	+0.05	+0.05**	+0.10	-0.27	—
edouardi	Marojejy-Kely	-0.51**	-0.07	+0.07	+0.05*	—	-0.32**	—
edouardi	Ambatosoratra	—	—	—	+0.02	+0.08	+0.30*	-0.03
edouardi	Anjanaharibe	-0.16	—	—	+0.05**	+0.09	+0.12*	-0.02
edouardi	Tsaratana	+0.17	—	—	—	—	-0.07	-0.05*
ambrensis	Mt. d’Ambre	-0.17*	-0.05	—	—	-0.04	+0.13	—

of Natural History, University of Florida, Gainesville (UF); the Australian Museum, Sydney (AMS); the Muséum national d'Histoire naturelle, Paris (MNHN, which does not assign catalogue numbers to types); and the Academy of Natural Sciences of Philadelphia (ANSP). Abbreviations: ad adult(s), juv juvenile(s).

Fischerpietteus edouardi Emberton, sp. nov.

(Figures 1–13)

Diagnosis: Differs from *F. ambrensis*, sp. nov. by its (a) looser coiling for the same spire height and higher spire for the same coiling, (b) larger aperture for same whorl count, (c) narrower umbilicus for the same diameter, (d) stronger rib sculpture on the shell periphery, and (e) absence of a spiral groove at the suture. Differs from *F. ankaranae*, sp. nov. by its (a) looser coiling for the same spire height, and (b) weaker rib sculpture at the suture. Differs from *F. vohimarae*, sp. nov. by its (a) narrower umbilicus for the same diameter, and clear presence of both (b) embryonic sutural notches and (c) rib sculpture at post-embryonic suture.

Holotype: Station 260 (UF 285406, 1 ad), 13°50'S, 49°59'E, Madagascar, summit of Mount Ambalanirana, 561 m, rainforest, 3 September 1995.

Illustrated dry-collected paratypes: Stations 527 (UF 285415, 1 ad), 606 (UF 285407, 1 ad), 643 (UF 285409, 1 ad), 645 (UF 285408, 1 juv), 689 (UF 285403, 1 ad).

Illustrated live-collected paratypes: Stations 260 (UF 285589, 1 ad, 2 juv [ad dissected]), 608 (UF 285588, 3 ad [dissected]).

Other dry-collected paratypes: Stations 260 (UF 285495, 1 juv), 261 (UF 285513, 1 ad), 513 (UF 285479, 1 juv), 519 (ANSP 407926, 1 juv; MNHN, 1 juv; UF 285417, 1 juv; UF 285478, 4 juv), 524 (UF 285416, 1 juv; UF 285480, 3 juv), 527 (AMS C.203512, 1 juv; UF 285418, 1 juv), 593 (UF 285510, 2 juv), 605 (UF 285517, 1 ad, 1 juv), 606 (UF 285492, 5 juv), 609 (AMS C.203507, 1 ad; ANSP 407922, 1 ad; MNHN, 1 ad; UF 285506, 3 ad, 9 juv), 610 (UF 285501, 1 juv), 620 (UF 285500, 1 ad), 625 (UF 285498, 2 juv), 627 (UF 285516, 1 ad, 1 juv), 629 (UF 285514, 3 ad, 1 juv), 631 (UF 285511, 3 ad, 5 juv), 633 (UF 285507, 3 juv), 634 (UF 285494, 1 ad, 5 juv), 638 (UF 285508, 1 ad, 2 juv), 639 (UF 285498, 2 juv), 643 (UF 285515, 2 ad, 12 juv), 645 (UF 285504, 2 juv), 648 (UF 285509, 2 ad, 2 juv), 661 (UF 285502, 1 juv), 662 (UF 285497, 1 juv), 664 (UF 285491, 1 ad), 666 (UF 285512, 3 ad, 6 juv), 668 (UF 285505, 4 juv), 671 (UF 285493, 4 juv), 673 (UF 285496, 1 ad), 674 (UF 285503, 1 ad, 3 juv), 688 (UF 285483, 2 juv), 689 (AMS C.203510, 1 ad; MNHN, 1 ad; UF 285405, 1 ad; UF 285486, 1 ad, 1 juv), 692 (UF 285488, 2 ad), 695 (UF 285484, 1 ad, 1 juv), 699 (ANSP 407924, 1 ad), 700 (UF 285404, 1 ad; UF 285485, 1 juv), 701

(UF 285489, 2 juv), 702 (UF 285490, 2 juv), 709 (UF 285402, 1 juv; UF 285487, 1 juv).

Other live-collected paratypes: Stations 262 (UF 285545, 1 ad [dried]), 587 (UF 285564, 1 ad), 593 (UF 285565, 1 ad), 597 (UF 285562, 1 ad), 601 (UF 285554, 1 ad), 605 (UF 285561, 1 juv), 606 (UF 285548, 1 ad, 2 juv [dried]), 607 (UF 285549, 2 ad, 3 juv), 608 (UF 285587, 5 ad, 14 juv), 609 (UF 285551, 3 ad, 6 juv), 610 (UF 285546, 1 juv [dried]), 625 (UF 285556, 1 ad), 629 (UF 285542, 2 ad [dried]), 631 (UF 285552, 3 juv), 633 (UF 285559, 2 juv), 634 (UF 285557, 4 juv), 636 (UF 285555, 1 juv), 638 (UF 285563, 2 juv), 643 (UF 285543, 2 ad, 5 juv [dried]), 648 (UF 285547, 1 juv [dried]), 659 (UF 285558, 1 juv), 661 (UF 285560, 1 ad), 666 (UF 285553, 1 ad), 668 (UF 285544, 1 juv [dried]), 671 (UF 285541, 2 ad, 2 juv [dried]), 673 (UF 285550, 1 ad), 674 (UF 285540, 1 ad, 1 juv [dried]), 689 (UF 285532, 1 juv [dried]), 694 (UF 285531, 1 juv [dried]), 696 (UF 285527, 1 juv [dried]), 700 (UF 285528, 1 juv [dried]), 701 (UF 285530, 1 juv [dried]), 709 (UF 285529, 1 ad [dried]).

Description of holotype shell (Figure 1): Diameter 3.71 mm, height 2.81 mm, whorls 5.55, umbilicus 1.00 mm. Spire domed-conic. Body-whorl periphery rounded; suture deeply impressed, simple; whorl shoulders rounded. Aperture circular, inside width 1.38 mm, no downward deflection. Apertural lip unreflected. Embryonic whorls 1.90; first 1.5 whorls 0.68 mm in diameter. Body-whorl sculpture consisting of fairly regular axial riblets, moderate in strength at suture, periphery, and umbilicus. Color whitish, translucent, with very faint yellow-green cast.

Embryonic shell sculpture of paratype from type locality: Smooth first 1.3 whorls, then sutural notches.

Shell variation, based on 35 shells from 18 stations in six transects (Tables 1, 2; Figures 1–4): Diameter to 4.63 mm, height/diameter 0.56–0.79, whorls to 5.65, coiling tightness (whorls/ ln diameter) 3.34–4.31, umbilicus/diameter 0.23–0.32, apertural inside width/whorl count 0.24–0.33. Embryonic whorls 1.80–2.10, diameter of first 1.5 whorls 0.68–0.83 mm. Embryonic sculpture: sutural notches first appearing at 1.0–1.7 whorls, axial grooves absent to moderate, spiral lines absent to moderate. Body-whorl axial ribs: moderate at suture, moderate to strong at periphery, weak to moderate at umbilicus.

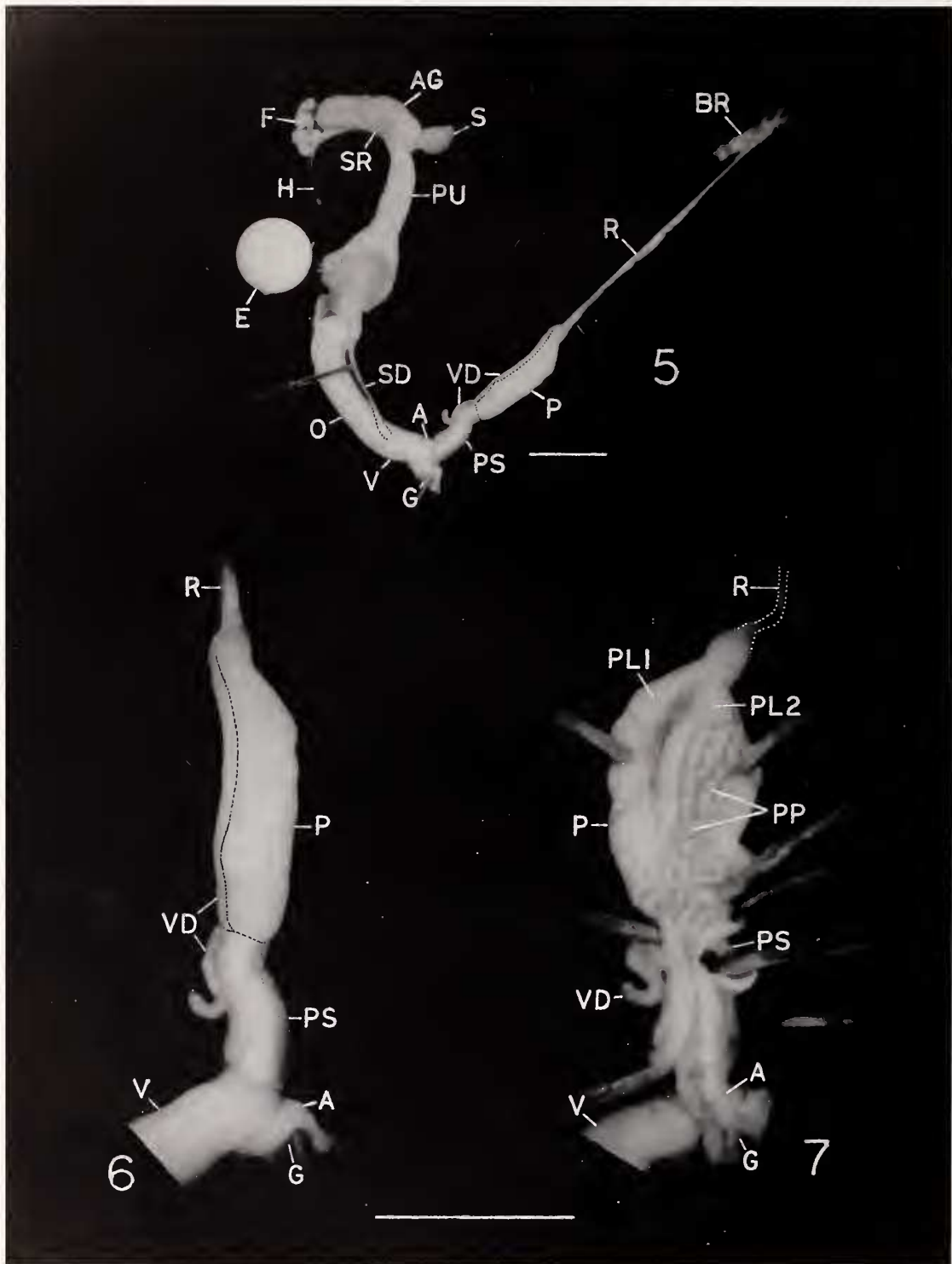
Variation strongly associated with altitude (Tables 1 and 2, Figures 2–4).

Anatomy: As described above for the genus (Figures 5–13).

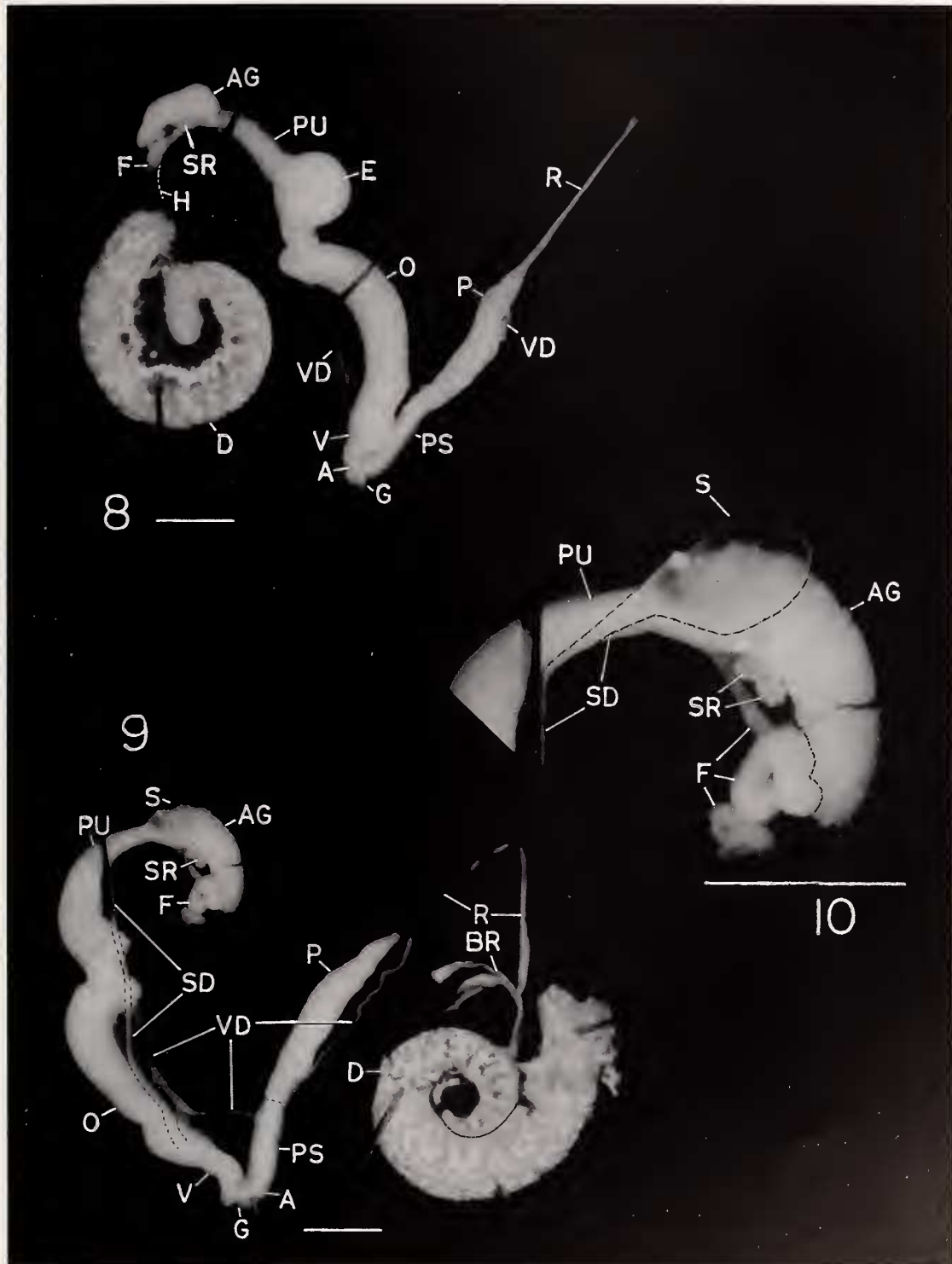
Etymology: For the late Edouard Fischer-Piette.



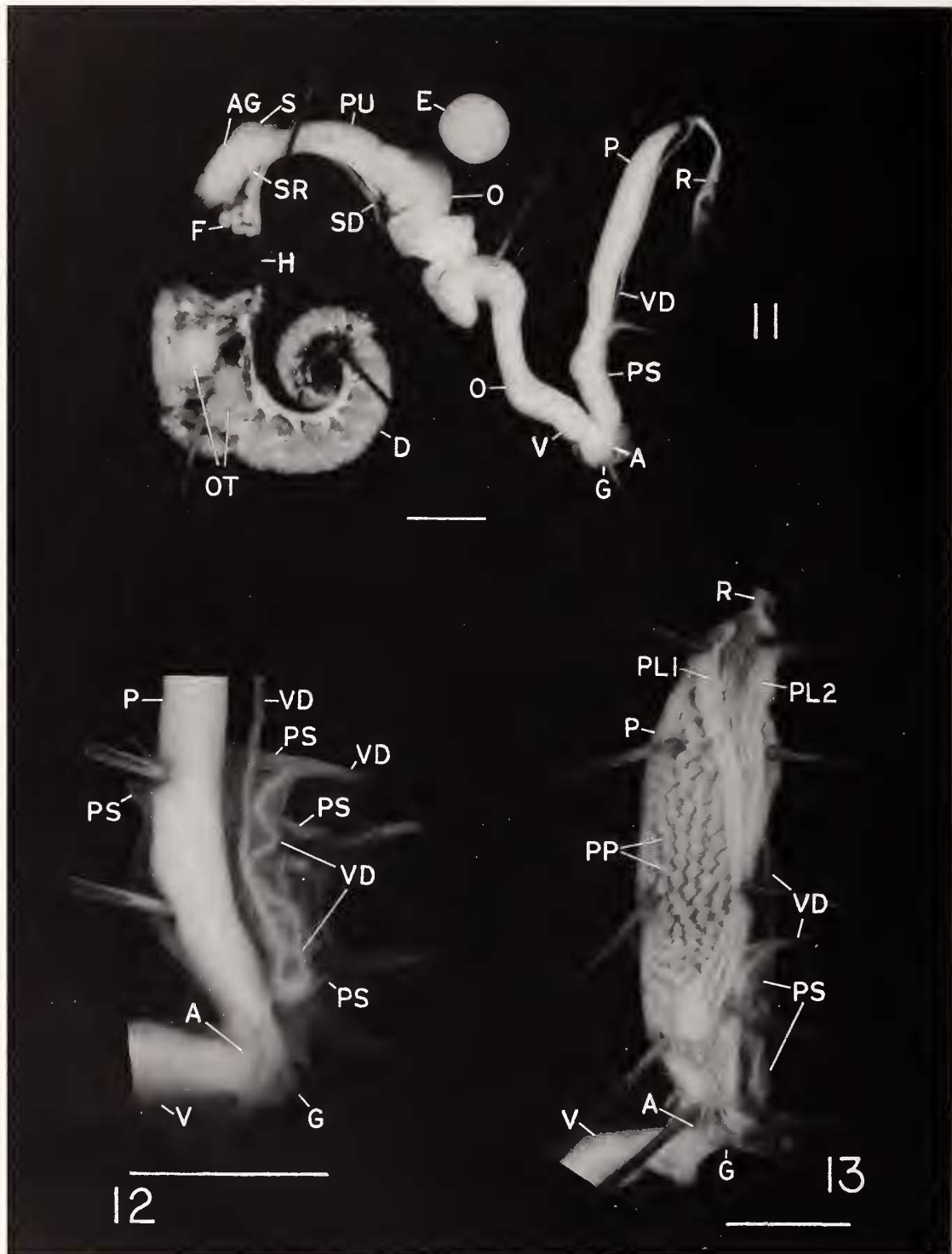
Figures 1–4. Shell variation in *Fischerpietteus edouardi* Emberton, sp. nov. Figure 1. Holotype in three views, UF 285406, station 260, summit Mt. Ambalanirana, 561 m. Figures 2, 3. Paratypes in two views. Figure 2. UF 285403, station 689, Mt. Anjanaharibe-Anivo, 1300 m. Figure 3. UF 285415, station 527, W. Tsaratanana Reserve, 1395 m. Figure 4. Three paratypes in one view: left, UF 285407, station 606, Mt. Marojejy, 1100 m; center, UF 285409, station 643, Mt. Marojejy-Kely, 1085 m; right, UF 285408, station 645, Mt. Marojejy-Kely, 960 m. Scale bar = 1 mm. (See Tables 1 and 2 for altitudinal trends of shell variation in this species.)



Figures 5-7. Anatomy of *Fischerpietteus edouardi* Emberton, sp. nov. paratype adult from type locality, summit of Mt. Ambalanirana, UF 285589. Figure 5. Reproductive system. Figures 6, 7. Penis undissected (Figure 6) and dissected to show sculpture of functional surface (Figure 7). Scale bars = 1 mm. Abbreviations for these and Figures 8-13: A, atrium; AG, albumen gland; BR, body retractor muscle; D, digestive gland; E, egg; F, fertilization pouch; G, genital pore; H, hermaphroditic duct; O, free oviduct; OT, ovotestes (hermaphroditic gland); P, penis; PL1, penial pilaster #1; PL2, penial pilaster #2; PP, penial pustules, each bearing a chitinous hook; PS, penial sheath; PU, prostate-uterus; R, penial retractor muscle; S, spermatheca; SD, spermathecal duct; SR, seminal receptacle; V, vagina; VD, vas deferens.



Figures 8–10. Anatomies of *Fischerpietteus edouardi* Emberton, sp. nov. paratype adults from station 608, Mt. Marojej, 1000 m, UF 285588. Figures 8, 9. Reproductive systems of two specimens. Figure 10. Enlargement of albumen-gland region of Figure 9. Scale bars = 1 mm. Abbreviations: see explanation of Figures 5–7.



Figures 11-13. Anatomy of *Fischerpietteus edouardi* Emberton, sp. nov. third paratype adult (specimen #3) from station 608, Mt. Marojejy, 1000 m, UF 285588. Figure 11. Reproductive system. Figure 12. Penial sheath opened to reveal course of the vas deferens. Figure 13. Penis opened to show functional surface. Scale bars = 1 mm. Abbreviations: see explanation of Figures 5-7.

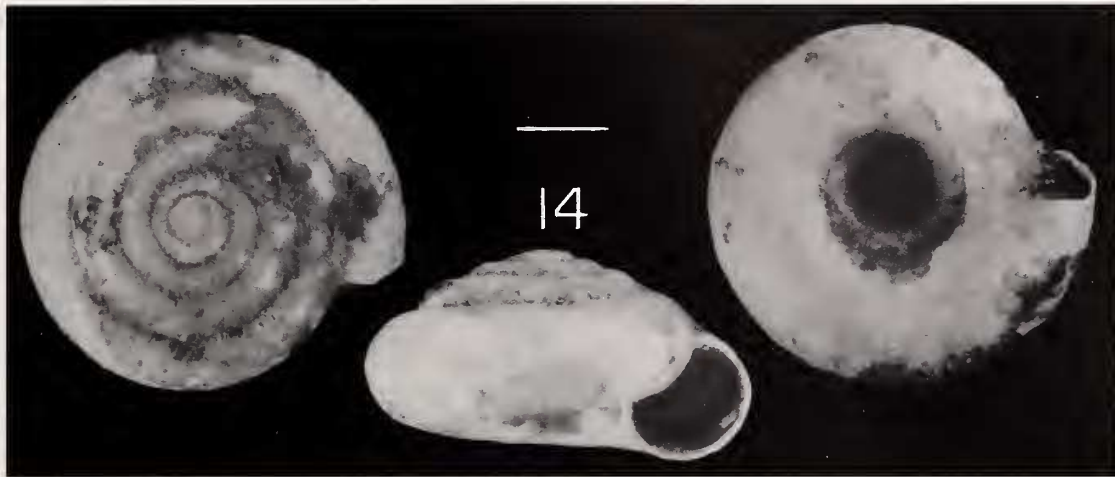


Figure 14. *Fischerpietteus vohimarae* Emberton, sp. nov. holotype in three views, UF 285414, station 257, south of Vohimar, 70 m. Scale bar (same as Figures 1–4) = 1 mm.

Fischerpietteus vohimarae Emberton, sp. nov.

(Figure 14)

Diagnosis: Differs from *F. edouardi* sp. nov. by its (a) broader umbilicus for the same diameter, and absence to extreme faintness of both (b) embryonic sutural notches and (c) rib sculpture at post-embryonic suture. Differs from *F. ambrensis* sp. nov. by its (a) looser coiling and (b) absence of spiral groove at suture.

Holotype: Station 257 (UF 285414, 1 ad), 13°35'S, 49°59'E; Madagascar, S of Vohimar, 70 m, viny rainforest, 2 September 1995.

Live-collected paratype: Station 256 (UF 285539, 1 ad [dried]).

Description of holotype shell: Diameter 4.34 mm, height 2.31 mm, whorls 5.35, umbilicus 1.59 mm. Spire low domed-conic. Body-whorl periphery rounded; suture deeply impressed, simple; whorl shoulders rounded. Aperture circular, inside width 1.31 mm, no downward deflection. Apertural lip unreflected. Embryonic whorls 1.90; first 1.5 whorls 0.74 mm in diameter. Embryonic sculpture virtually smooth. Body-whorl sculpture nearly smooth, with weak traces of axial ribs. Color whitish, translucent, with very faint yellow-green cast; opaque white where periostracum eroded.

Shell variation, based on two shells from two stations in one transect (Table 1): Diameter to 4.34 mm, height/diameter 0.53–0.59, whorls to 5.40, coiling tightness (whorls/ ln diameter) 3.64–3.90, umbilicus/diameter 0.36–0.37, apertural inside width/whorl count 0.25. Embryonic whorls 1.90, diameter of first 1.5 whorls 0.74–0.75 mm. Embryonic sculpture: sutural notches first appearing at 1.5 whorls, axial grooves slight to moderate, spiral lines

absent. Body-whorl axial ribs: very weak at suture, weak at periphery, very weak at umbilicus.

Etymology: For the coastal city of Vohimar, near the type locality.

Fischerpietteus ambrensis Emberton, sp. nov.

(Figure 15)

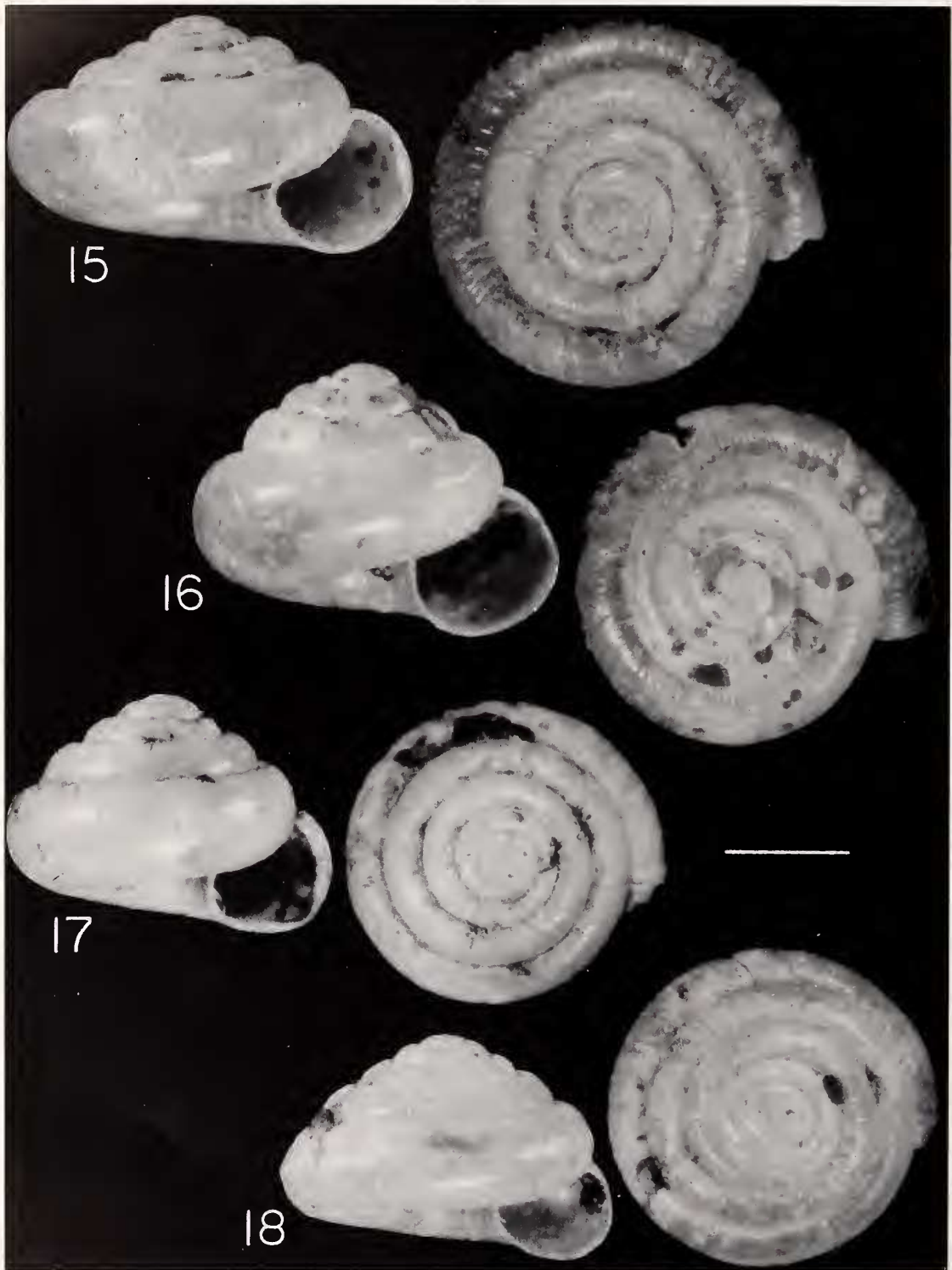
Diagnosis: Differs from *F. edouardi* sp. nov. by its (a) tighter coiling for same spire height and lower spire for same coiling, (b) smaller aperture for same whorl count, (c) broader umbilicus for same diameter, (d) weaker rib sculpture on shell periphery, and (e) presence of spiral groove at suture. Differs from *F. ankaranae*, sp. nov. by its (a) lower spire height and (b) broader umbilicus for same coiling, and (c) weaker rib sculpture at the suture. Differs from *F. vohimarae*, sp. nov. by its (a) tighter coiling and (b) presence of spiral groove at suture.

Holotype: Station 194 (UF 285410, 1 ad), 12°34'S, 49°09'E, Madagascar: Montagne d'Ambre, 1280 m, rainforest, 12 July 1995.

Dry-collected paratypes: Stations 169 (UF 285537, 1 ad), 172 (UF 285411, 1 ad; UF 285523, 2 ad), 188 (UF 285522, 1 ad), 193 (UF 285412, 1 juv; UF 285521, 1 juv), 418 (AMS C.203509, 5 ad; ANSP 407923, 5 ad; MNHN, 5 ad; UF 285413, 3 ad; UF 285520, 97 ad, 157 juv).

Live-collected paratypes: Stations 169 (UF 285537, 1 ad [dried]), 172 (UF 285538, 3 ad, 4 juv [dried]), 193 (UF 285535, 1 juv [dried]), 418 (UF 285536, 2 ad, 1 juv [dried]).

Description of holotype shell: Diameter 3.16 mm, height 1.88 mm, whorls 4.85, umbilicus 1.11 mm. Spire low-



Figures 15–18. Holotypes in two views. Figure 15. *Fischerpietteus ambrensis* Emberton, sp. nov., UF 285410, station 194, Montagne d'Ambre National Park, 1280 m. Figure 16. *Fischerpietteus ankaranae* Emberton, sp. nov., UF 285401, station 565, Ankarana Reserve, 40 m. Figure 17. *Fischerpietteus ambatovakiae* Emberton, sp. nov., UF 285400, station 758, Ambatovaky Reserve, 605 m. Figure 18. *Fischerpietteus minutus* Emberton, sp. nov., UF 285419, station 526, Tsaratanana Reserve, 1500 m. Scale bar (56% larger than in Figures 1–4 & 14) = 1 mm.

conic. Body-whorl periphery rounded; suture deeply impressed, within a pronounced spiral groove; whorl shoulders rounded. Aperture circular, inside width 1.06 mm, no downward deflection. Apertural lip unreflected. Embryonic whorls 1.90; first 1.5 whorls 0.74 mm in diameter. Body-whorl sculpture consisting of fairly regular axial riblets, weak-to-moderate in strength at the suture, and weak at the periphery and umbilicus. Color whitish, translucent, with a very faint yellow-green cast. Embryonic sculpture smooth to 1.3 whorls, then with sutural notches and with a trace of spiral lines.

Shell variation, based on nine shells from five stations in three transects (Tables 1, 2): Diameter to 3.45 mm, height/diameter 0.54–0.63, whorls to 5.55, coiling tightness (whorls/ \ln diameter) 4.01–4.48, umbilicus/diameter 0.32–0.38, apertural inside width/whorl count 0.19–0.23. Embryonic whorls 1.85–1.95, diameter of first 1.5 whorls 0.66–0.79 mm. Embryonic sculpture: sutural notches first appearing at 1.1–1.5 whorls, axial grooves absent to slight, spiral lines absent to very slight. Body-whorl axial ribs: weak to moderate at suture, weak at periphery, very weak to weak at umbilicus.

Variation on Montagne d'Ambre strongly associated with altitude (Table 2). Population at Andavakoera with weaker sutural groove, weaker axial ribs in umbilical region, slightly tighter embryonic coiling (diameter of first 1.5 whorls), slightly broader umbilicus (Table 1), and very faint embryonic sutural notches, so may merit designation as subspecies.

Etymology: For Montagne d'Ambre National Park.

Fischerpietteus ankaranae Emberton, sp. nov.

(Figure 16)

Diagnosis: Differs from *F. edouardi* sp. nov. by its (a) tighter coiling for the same spire height, and (b) stronger rib sculpture at the suture. Differs from *F. ambrensis* sp. nov. by its (a) higher spire height and (b) narrower umbilicus for same coiling, and (c) stronger rib sculpture at the suture.

Holotype: Station 565 (UF 285401, 1 ad), 12°55'S, 49°05'E, Madagascar, Ankarana Reserve, 40 m, dry deciduous forest, 22 August 1995.

Paratypes: None.

Description of holotype shell: Diameter 2.88 mm, height 2.02 mm, whorls 4.75, umbilicus 0.75 mm. Spire domed-conic. Body-whorl periphery rounded; suture deeply impressed, simple; whorl shoulders rounded. Aperture circular, inside width 1.08 mm, no downward deflection. Apertural lip unreflected. Embryonic whorls 1.80; first 1.5 whorls 0.76 mm in diameter. Embryonic sculpture initially smooth, then with pronounced sutural notches. Body-whorl sculpture consisting of fairly regular axial

riblets, moderate in strength at suture, but weak at periphery and umbilicus. Color whitish, translucent, with very faint yellow-green cast.

Shell variation: Unknown.

Comment: Although known only from a single shell, falling sufficiently outside ranges of variation of other species (Table 1) to merit recognition as distinct species.

Etymology: For Ankarana Reserve.

Fischerpietteus ambatovakiae Emberton, sp. nov.

(Figure 17)

Diagnosis: Unique within the genus for embryonic sutural notches that appear immediately, at 0.0 whorls. Further differs from *F. minutus*, sp. nov. by its looser coiling and rounded periphery. Further differs from all other species by its tighter coiling.

Holotype: Station 758 (UF 285400, 1 ad), 16°42'S, 49°10'E, Madagascar, Ambatovaky Reserve, 605 m, rain-forest. 23 November 1995.

Dry-collected paratypes: Stations 756 (AMS C.203508, 1 juv; UF 285518, 1 juv), 758 (UF 285519, 1 juv).

Description of holotype shell: Diameter 2.55 mm, height 1.83 mm, whorls 5.00, umbilicus 0.69 mm. Spire conic, slightly domed. Body-whorl periphery rounded; suture deeply impressed, simple; whorl shoulders rounded. Aperture circular, inside width 0.93 mm, no downward deflection. Apertural lip unreflected. Embryonic whorls 1.95; first 1.5 whorls 0.68 mm in diameter. Body-whorl sculpture consisting of fairly regular axial riblets, moderate in strength at suture and periphery, weak at umbilicus. Color whitish, translucent, with faint yellow cast.

Embryonic shell sculpture of paratype: Sutural notches beginning immediately, at 0.0 whorl. Slight axial grooves evident.

Shell variation, based on two shells from two stations in one transect (Table 1): Diameter to 2.55 mm, height/diameter 0.61–0.72, whorls to 5.00, coiling tightness (whorls/ \ln diameter) 5.21–5.34, umbilicus/diameter 0.23–0.27, apertural inside width/whorl count 0.17–0.20. Embryonic whorls 1.85–1.95, diameter of first 1.5 whorls 0.68–0.70 mm. Embryonic sculpture: sutural notches first appearing at 0.0 whorls (based only on paratype, as holotype apex too eroded), axial grooves slight, spiral lines absent. Body-whorl axial ribs: moderate at suture, moderate at periphery, weak at umbilicus.

Etymology: For Ambatovaky Reserve.

Fischerpietteus minutus Emberton, sp. nov.

(Figure 18)

Diagnosis: Unique within the genus for its extremely tight coiling. Further differs from *F. ambatovakiae*, sp.

nov. by embryonic sutural notches first appearing at 0.7–0.8 whorl and by its slightly angulate shell periphery.

Holotype: Station 526 (UF 285419, 1 ad), 13°59'S, 48°47'E, Madagascar, western Tsaratanana Reserve, 1500 m, rainforest, 17 June 1995.

Dry-collected paratypes: Stations 609 (UF 285420, 1 juv; UF 285481, 2 ad, 2 juv), 649 (AMS C. 203511, 1 ad; ANSP 407925, 1 ad; MNHN, 1 ad; UF 285421, 2 ad; UF 285482, 4 ad, 15 juv).

Live-collected paratypes: Stations 526 (UF 285534, 1 juv [dried]), 609 (UF 285533, 7 ad, 6 juv [dried]).

Description of holotype shell: Diameter 2.67 mm, height 1.72 mm, whorls 5.35, umbilicus 0.84 mm. Spire domed-conic. Body-whorl periphery with slight peripheral angulation; suture deeply impressed, simple; whorl shoulders rounded. Aperture circular, inside width 0.89 mm, no downward deflection. Apertural lip unreflected. Embryonic whorls 1.95; first 1.5 whorls 0.63 mm in diameter. Embryonic sculpture smooth to 0.75, then sutural notches and slight traces of both axial grooves and spiral lines. Body-whorl sculpture consisting of fairly regular axial riblets, moderate in strength at suture, periphery, and umbilicus; trace of minute, evenly spaced, incised, spiral lines, most evident on the base of the shell under high magnification. Color whitish, translucent, with very faint yellow-green cast.

Shell variation, based on eight shells from three stations in three transects (Table 1): Diameter to 2.67 mm, height/diameter 0.60–0.74, whorls to 5.80, coiling tightness (whorls/*ln* diameter) 5.45–6.34, umbilicus/diameter 0.27–0.32, apertural inside width/whorl count 0.15–0.17. Embryonic whorls 1.90–2.00, diameter of first 1.5 whorls 0.63–0.68 mm. Embryonic sculpture: sutural notches first appearing at 0.70–0.80 whorls, axial grooves slight to moderate, spiral lines absent to moderate. Body-whorl axial ribs: moderate at suture, moderate at periphery, weak to moderate at umbilicus.

Shells from the two Marojejy transects differ from type-locality (Tsaratanana) shells by their substantially tighter coilings (whorls/*ln* diameter), higher spires (height/diameter, and smaller apertures (aperture/whorls), that fall somewhat beyond altitudinal differences within *F. edouardi*, sp. nov. (Tables 1, 2), so may represent a distinct subspecies.

Etymology: For the minute size (Latin “*minutus*”).

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LITERATURE CITED

- BRUGGEN, A. C. VAN. 1967. An introduction to the pulmonate family Streptaxidae. *Journal of Conchology*, London 26: 181–188.
- BRUGGEN, A. C. VAN. 1989. Studies on *Parrennea* (Mollusca, Gastropoda Pulmonata, Streptaxidae) additional to the revision by Adam & Van Goethem, 1978. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C* 92:1–56.
- EMBERTON, K. C. 1994. Thirty new species of Madagascan land snails. *Proceedings of the Academy of Natural Sciences of Philadelphia* 145:147–189.
- EMBERTON, K. C. 1999. *Edentulina* of Madagascar (Pulmonata: Streptaxidae). *American Malacological Bulletin* 15:97–108.
- EMBERTON, K. C. 2001a. Dentate *Gulella* of Madagascar (Pulmonata: Streptaxidae). *American Malacological Bulletin* 16: 71–129.
- EMBERTON, K. C. 2001b. Exploratory phylogenetic and biogeographic analyses within three land-snail families in south-eastern-most Madagascar. *Biological Journal of the Linnean Society* 72:567–584.
- EMBERTON, K. C. 2002. *Parvedentulina* and edentate *Gulella* of Madagascar (Pulmonata: Streptaxidae). *Archiv für Molluskenkunde* 131:67–165.
- EMBERTON, K. C. & T. A. PEARCE. 2000. Small high-spired land pulmonates from Mounts Mahermana, Ilapiry, and Vasiha, southeastern Madagascar, with description of a new genus and with conservation statuses of 15 streptaxids. *The Veliger* 43:126–153.
- EMBERTON, K. C., T. A. PEARCE & R. RANDALANA. 1996. Quantitatively sampling land-snail species richness in Madagascar rainforests. *Malacologia* 38:203–212.
- FISCHER-PIETTE, E., C. P. BLANC, F. BLANC & F. SALVAT. 1994. Gastéropodes terrestres pulmonés. *Faune de Madagascar* 83: 1–551.
- GERLACH, J. 1995. The taxonomy and affinities of the genus *Priodiscus* (Mollusca: Gastropoda: Streptaxidae). *Journal of Conchology*, London 35:357–368.
- GERLACH, J. & A. C. VAN BRUGGEN. 1999. Streptaxidae of the Seychelles Islands, western Indian Ocean. *Zoologische Mededelingen uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden* 328:1–60.
- NORDSIECK, H. 1986. The system of the Stylommatophora (Gastropoda), with special regard to the systematic position of the Clausiliidae, II. Importance of the shell and distribution. *Archiv für Molluskenkunde* 117:93–116.
- PONDER, W. F. & D. R. LINDBERG. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society* 119: 83–265.
- TEMPLETON, A. R. 1989. The meaning of species and speciation: A genetic perspective Pp. 3–27 in D. Otte & J. A. Endler (eds.). *Speciation and Its Consequences*. Sinauer Associates: Sunderland, Massachusetts.
- TILLIER, S. 1989. Comparative morphology, phylogeny and classification of land snails and slugs (Gastropoda: Pulmonata: Stylommatophora). *Malacologia* 30:1–303.
- VAUGHT, K. C. 1989. *A Classification of the Living Mollusca*. American Malacologists Inc.: Melbourne, Florida.
- VERDCOURT, B. 1990. Two Ethiopian streptaxids (Gastropoda: Pulmonata: Streptaxidae). *Journal of Conchology*, London 33:345–354.
- ZILCH, A. 1959–1960. *Gastropoda. Teil 2. Euthyneura. Band 6*. Pp. 1–834 in O. H. Schindewolf (ed.), *Handbuch der Paläozoologie*. Gebrüder Bornträger: Berlin.